

EFFECTS OF PARASITIC FLIES (*PROTOCALLIPHORA* SPP.) ON NESTLINGS OF MOUNTAIN AND CHESTNUT-BACKED CHICKADEES

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Protocalliphora (Diptera: Calliphoridae) larvae are hematophagous parasites which attack the nestlings of a broad range of nidicolous birds. The genus is widespread geographically and is found in many habitats. Despite the fact that nest infestations are common, only limited biological information and even less quantitative information exists on these flies. In part this can be attributed to difficulties and limitations imposed by working in active nests without undue disturbance of the birds and to the lack of success of rearing the flies in a laboratory situation.

During the course of a long-term study on the population biology of Chestnut-backed (*Parus rufescens*) and Mountain (*Parus gambeli*) chickadees we have noted that most nests were infested by *Protocalliphora* and that these infestations frequently exceeded 100 parasites per nest. For this reason we became interested in what effects *Protocalliphora* larvae have on the survivorship of their hosts.

Apparently, larvae of all *Protocalliphora* spp. feed solely on blood of birds. Because purely hematophagous diets are deficient in the vitamin B complex (Fraenkel 1952) the diet may be supplemented by the action of gut symbiotes or from other food sources, such as yeast, in the nest (K. S. Hagen, pers. comm.). With the exception of *Protocalliphora hirudo*, which lives subcutaneously, the larvae of all Nearctic species are intermittent ectoparasites living largely in the nest material (Zumpt 1965, Bédard and McNeil 1979). *Protocalliphora hirudo* is known to remain briefly on birds after fledging (Zumpt 1965). *Protocalliphora* is the only North American genus of Diptera with hematophagous larvae (Zumpt 1965).

Opinions in the literature regarding the effects of *Protocalliphora* on nestling birds are mixed and in most instances inconclusive. Nestling mortality attributed to *Protocalliphora* has been widely reported. Early reports have been summarized by Bennett (1957). However, direct evidence demonstrating that *Protocalliphora* was, in fact, the cause of death was not provided in any of these studies. It appears that in most cases the parasite simply provided the most convenient explanation to account for nestling mortality.

Observations by others indicated that little or no nestling mortality was found in infested nests even when *Protocalliphora* numbers ranged into the hundreds per nest (Rothschild and Clay 1952). Bennett (1957) studied

2519 nests and found nestling mortality to be slight, and similar between infested and uninfested nests. Whitworth (1976) examined 1819 nests, and although finding greater nestling mortality than Bennett, concluded that *Protocalliphora* was only one of several stresses encountered by birds and was not directly responsible for these deaths. Eschuis-van der Voet and Kluyver (1971) noted in a progress report a relationship between timing and intensity of *Protocalliphora* infestation and first year survival of Great Tits (*Parus major*); unfortunately this study was never published.

In our study, previously established nestbox plots provided a substantial number of accessible nests to investigate the biology of *Protocalliphora* spp. parasitizing Mountain and Chestnut-backed chickadees. In this paper we will examine the relationship between intensity of *Protocalliphora* infestations and chickadee fledging rates. In this respect we were interested in seeing if there might be some threshold value of *Protocalliphora* numbers above which chickadee nestlings would succumb. Finally, we hypothesized that chickadees fledging from heavily infested nests would do so in a weakened condition. Since chickadees will fledge prematurely if disturbed during the latter part of the nestling period and because it was logistically impossible to follow fledglings, we attempt to look at this question through the more indirect means of relating larval biomasses to weakening of birds through pre-fledging blood loss.

STUDY AREAS AND METHODS

Three nestbox plots were established in 1966 in Modoc National Forest, Modoc Co., California. This forest is mixed conifer stands dominated by ponderosa pine (*Pinus ponderosa*) and white fir (*Abies concolor*) with a lesser amount of incense cedar (*Calocedrus decurrens*) also present. The elevation of the study sites ranged from 1625–1900 m. Each plot was formed by the placement of boxes in a grid pattern with 10 east-west parallel rows of five boxes each. All boxes were placed on trees at breast height (1.5 m) and spaced at intervals of 100 m. Prior to the 1976 breeding season additional boxes were placed in half of one plot by reducing the distance between boxes to 50 m. The nestboxes used in this study were constructed of cement and sawdust and were purchased from Schwegler and Sons of Munich, Germany. The entrance hole was 3.3 cm, the interior depth beneath the hole was 12 cm, and the inside diameter was 11 cm.

In 1972 three more nestbox plots were set up in an identical manner at Blodgett Forest Research Station, 19.5 km east of Georgetown, El Dorado Co., California. Blodgett Forest (elev. 1250–1400 m) is 1215 ha of second growth mixed conifer stands. Major tree species present are ponderosa pine, sugar pine (*Pinus lambertiana*), white fir, incense cedar, black oak (*Quercus kelloggii*), and tan oak (*Lithocarpus densiflora*).

In February 1978, 100 boxes were placed on East Bay municipal land, in Contra Costa County, California, situated immediately east of Tilden Park. Boxes were placed a minimum of 50 m apart without regard to pattern. Forty-nine of these boxes were placed in even-aged plantations of Monterey pine (*Pinus radiata*) essentially pure in character, although some California bay (*Umbellularia californicus*) was present. The remaining 51 boxes were placed in stands of California live oak (*Quercus agrifolia*) with lesser amounts of California bay, interior live oak (*Q. wislizenii*), and big leaf maple (*Acer macrophyllum*). Prior to 1979, 16 of

these latter boxes were removed from an area of no nesting to replace old boxes in Modoc County and Blodgett Forest.

Active nests were checked at least once every three days. Bird nesting data included number of nestlings, fledging success, and notations on any unusual appearance in the health of the birds. The fledging period of Mountain and Chestnut-backed chickadees is 21 days: after the nestlings were 15 days old, only their presence or absence was noted to avoid premature fledging. Nestling mortality after this period was assessed by examining fledged nests for dead birds.

Most nests were collected within 3 weeks after fledging and placed in emergence containers. The number of emerging flies and their hymenopterous parasitoids were then counted. After emergence was completed puparia were counted. Because of difficulty in locating all puparia, the number of emerged puparia counted was usually less than the number of reared flies. In some cases it was greater, indicating that some flies had emerged prior to nest collection. Thus, for establishment of infestation number in a nest, the larger number was used and added to the number of unemerged puparia.

A series of nest substitutions was made by taking uninfested nests collected from the Contra Costa County nestbox plots, cleaning them of arthropods in Berlese funnels, and then exchanging them for active nests in the Blodgett County and Modoc County nestbox plots. The active box was removed from the tree and replaced by a box containing the clean nest. The nestlings were then examined for *Protocalliphora* and transferred to this new nest. This process allowed for the determination of oviposition times and provided *Protocalliphora* larvae for assessment of biomass. The larvae were held for 48 h prior to weighing to allow for assimilation or voiding of gut contents.

RESULTS

Dahlsten and Copper (1979) have summarized the breeding data collected over a 10-year span for the Mountain Chickadee on the Modoc County nestbox plots and have gathered similar data for both species of chickadee for Blodgett Forest plots (Dahlsten and Copper, unpubl.). Mean annual fledging success for Mountain Chickadees in Modoc County study plots was 70.2%. This figure was obtained by dividing the total number of birds fledging by the number of eggs in completed clutches (e.g., where incubation had begun). In addition, since breeding chickadees in our study sites show strong nest-site fidelity from year-to-year, we have been able to use banding returns to estimate a first year mortality of 85% for fledglings. This figure is not unusually high for a small passerine (Welty 1962). It is believed that much of the high first year mortality in passerines occurs within the first few weeks after fledging (Lack 1966).

The Contra Costa County nestboxes were visited every 3 days in 1978, but only once a month in 1979. The late date at which the nestbox plot was established may have reduced box usage the first year as the first Chestnut-backed Chickadee egg was laid within 3 weeks of this time. In 1978 there were 19 Chestnut-backed Chickadee nesting efforts reaching the nestling stage while in 1979 there were 29. An additional seven chick-

adee nests were available during these 2 years from boxes in nearby Albany and Orinda, California. With the exception of one case of vandalism, fledging occurred from all of these nests; there were no instances of predation. In 1978 all chickadee nests were free of *Protocalliphora*; however, a Bewick's Wren (*Thryomanes bewickii*) nest in one of the boxes contained 50 *Protocalliphora* puparia. The following year one chickadee nest was found to be infested with *Protocalliphora*. This nest contained 104 puparia although for an unknown reason only 12 flies emerged.

In 1977 clutches in 25 nests hatched at Blodgett Forest, of which 20 successfully fledged. Three of the successful nests were of Chestnut-backed Chickadees and the remainder were of Mountain Chickadees. *Protocalliphora* data were taken for 19 of the successful nests and for two that failed prematurely due to nestling mortality. In 1978 11 successful Mountain Chickadee as well as two successful and one predated Chestnut-backed Chickadee nests taken from the nestbox plots were examined for *Protocalliphora*. An additional Chestnut-backed Chickadee nest taken from a snag near one nestbox plot was also collected. Finally, in 1979 an additional nine Mountain and two Chestnut-backed chickadee nests were collected. Young had fledged from all of these nests.

All of the chickadee nests from Blodgett Forest were infested during these 3 years with the exception of one Chestnut-backed Chickadee nest in 1977 and one Mountain Chickadee nest in 1978 (Table 1). In the latter case, larvae had been observed in the nest, but apparently none survived to the pupal stage. Considerable variation was found in the numbers of *Protocalliphora* per nest (Table 1), but there were no significant differences found between the species of the chickadees (Table 1).

In 1977, 97 Mountain Chickadee nests reached the nestling stage on the Modoc County study plots. Of these, nestlings fledged from 65 nests, and 32 terminated with the death of the nestlings. Predation by weasels (*Mus-tela* spp.) and snakes was responsible for most of the mortality in these instances although the cause of clutch failure in a few nests could not be determined. Forty-seven of the fledged nests and 26 of the unsuccessful ones were examined for *Protocalliphora* numbers.

In 1978, 80 nests reached the nestling stage and young were fledged from 77 of these. Weasel predation occurred in one nest when the young were 17 days old and in two others when the nestlings were about 15 days old.

Infestation numbers for successful nests during both years are summarized in Table 2. As in Blodgett Forest, nearly all nests were infested. Infestation numbers in nests terminated by predation or other nestling mortality during the first 2 weeks were extremely low; over 80% of these

TABLE 1
NUMBER OF *PROTOCALLIPHORA* INFESTING NESTS OF CHESTNUT-BACKED AND MOUNTAIN CHICKADEES AT BLODGETT FOREST, 1977-1979

	No. nests									
	1977		1978		1979					
(a) <i>Protocalliphora</i> in nest										
0	1		1		0					
1-19	4		3		0					
20-39	3		2		2					
40-59	4		0		1					
60-79	2		2		0					
80-99	1		2		1					
100+	4		4		7					
Total nests	19		14		11					
(b)	1977				1978				1979	
Nests	CBC ^a	MC ^b	Total	CBC	MC	Total	CBC	MC	Total	
Range	3	16	19	3	11	14	2	9	11	
Total larvae	36-273	0-17	0-273	112-144	0-173	0-173	22-133	20-238	20-238	
$\bar{x} \pm SD^c$	358	822	1180	398	562	951	155	1042	1197	
	119.3 \pm	51.4 \pm	62.1 \pm	129.7 \pm	51.1 \pm	67.9 \pm	77.5 \pm	115.8 \pm	108.8 \pm	
	133.2	50.4	68.8	16.3	54.2	58.5	78.5	64.8	67.9	

^a Chestnut-backed Chickadee.

^b Mountain Chickadee.

^c Differences between bird species not significant (2 sample *t*-tests, $P > 0.05$).

TABLE 2
INFESTATION NUMBERS OF *PROTOCALLIPHORA* IN NESTS OF MOUNTAIN CHICKADEES AT
MODOC COUNTY, 1977-1978

(a) <i>Protocalliphora</i> in nest	No. nests	
	1977	1978 ^a
0	3	6
1-19	26	29
20-39	8	20
40-59	5	9
60-79	3	4
80-99	1	4
100+	1	8
Total nests	47	80

(b)	1977	1978
Nests	47	80
Range	0-162	0-164
Total larvae	1093	2977
$\bar{x} \pm SD$	23.3 ± 31.3	37.2 ± 39.0

^a Includes three nests in which entire clutch was predated after attaining age of 15 days.

nest had fewer than 20 *Protocalliphora*. Thus, early host mortality led to a decrease in fly numbers, undoubtedly reducing the time available for oviposition as well as providing an insufficient period for larval development.

A series of over 250 adult *Protocalliphora* with their associated puparia and larvae were used for species determinations. These included material from both Chestnut-backed and Mountain chickadee nests and from all three study areas. With two exceptions, all *Protocalliphora* collected in or reared from chickadee nests belonged to a single new species (termed here *Protocalliphora* n.sp. no. 1). This species had previously been collected by Dahlsten at these study areas and in Inyo County, California. While he observed larvae each year since the study began, positive determinations were made only on material collected during the 1969 breeding season. This species was identified from nests of both species of chickadee as well as from that of a Red-breasted Nuthatch (*Sitta canadensis*) (Sabrosky, pers. comm.). Whitworth (1976) also collected this species in Utah, primarily from the nests of cavity nesting birds. In this study *Protocalliphora* n.sp. no. 1 was also reared from the nests of Brown Creepers (*Certhia familiaris*), a Bewick's Wren, and a Barn Swallow (*Hirundo rustica*), but it was not found in nests of Western Bluebirds (*Sialia mexicana*)

TABLE 3
MORTALITY IN NESTS OF CHESTNUT-BACKED AND MOUNTAIN CHICKADEES FLEDGING
YOUNG, BLODGETT FOREST, CALIFORNIA, 1977-1978

Study site and year	Nests examined	Number of nests	Nestlings hatched	Dead	Percent fledging ^a	Proto-calliphora per nestling	Estimated blood loss per nestling to <i>Proto-calliphora</i> (g) ^b
Blodgett 1977	With bird mortality ^c	4	22	5	77	3.5	0.44
	Most heavily infested	7	50	0	100a	17.8	2.23
	All successful nests ^d	19	120	5	96a	9.8	1.23
Blodgett 1978	With bird mortality	1	7	1	86	11.1	1.44
	Most heavily infested	5	35	0	100a	18.8	2.35
	All successful nests	6	93	1	99a	10.8	1.35

^a For year and site, pairs with different letters are statistically significant (1-sample *t*-test: $P > 0.05$).

^b Blood loss estimated at 0.125 g/larvae assuming average biomass per larvae as 0.05 g and conversion efficiency of blood to parasite biomass at 40%.

^c Nests in which mortality occurred, but at least one nestling fledged.

^d Nests fledging at least one young.

located within 10 m of infested chickadee nests. Instead, the bluebirds were hosts to *P. sialia*. Similar findings were also made by Whitworth (1976).

The exceptions included one individual of *P. hirundo* which was reared from the nest of a Mountain Chickadee at Blodgett Forest in 1978. This is likely an aberrant occurrence as this species normally attacks cup nesters (Bennett 1957). The second exception was a second new species of *Protocalliphora* which was also reared from a Mountain Chickadee nest at Blodgett Forest in 1979. At present we do not know if this species has been collected previously.

Protocalliphora n.sp. no. 1 is univoltine (producing but one generation each year) and perhaps for this reason infestation numbers did not increase as the nesting season progressed and nesting density declined. Oviposition by the flies occurs in the nest throughout the nestling stage but not before the first birds hatch. There are three larval instars, of which the first two are brief. The larvae are intermittent feeders and spend most of the time in or under the nest. Larval development may be completed before the nestlings fledge. Mature larvae enter a nonfeeding pre-pupal stage which lasts about 2 days. The pupation site is within the nest material. Details of the biology of *Protocalliphora* n.sp. no. 1 will be published elsewhere (Gold and Dahlsten, in press).

TABLE 4
MORTALITY IN THOSE NESTS OF MOUNTAIN CHICKADEES FLEDGING YOUNG, MODOC COUNTY, CALIFORNIA, 1977-1978

Study site and year	Nests examined	Number of nests	Nestlings hatched	Dead	Percent fledging ^a	<i>Proto-calliphora</i> per nestling	Estimated blood loss per nestling to <i>Proto-calliphora</i> (g) ^b
Modoc 1977	With bird mortality ^c	12	78	19	76	6.5	0.81
	Most heavily infested	7	45	4	91a	12.7	1.89
	All successful nests ^d	47	280	19	93a	3.9	0.49
Modoc 1978	With bird mortality	9	62	10	84	9.2	1.15
	Most heavily infested	15	111	8	93a	14.5	1.80
	All successful nests	80	488	10	98b	6.1	0.76

^a For year and site, pairs with different letters are statistically significant (1-sample *t*-test: $t = 5.96$, $df = 93$, $P < 0.01$).

^b Blood loss estimated at 0.125 g/larvae assuming average biomass per larvae as 0.05 g and conversion efficiency of blood to parasite biomass at 40%.

^c Nests in which mortality occurred but at least one nestling fledged.

^d Nests fledging at least one young.

Difficulties in working with cavity nests and the handling of older nestlings made direct measurements of parasite feeding effects untenable. Observations of the larvae feeding on the birds were uncommon and this feeding was easily disturbed. It is possible that most feeding occurred at night when the nestlings would be inactive. As an indirect means of assessing stress on nestlings, *Protocalliphora* larval biomasses were obtained to give a measure of parasite load. Weights of immature *Protocalliphora* were found to vary moderately. These weights were related to age and affected by gut contents. Maximal larval weights occasionally exceeded 100 mg and the average for third instar larvae was about 80 mg ($N = 170$). Prepupae averaged about 65 mg ($N = 20$) and the puparia weights ranged from 40-50 mg ($N = 40$).

DISCUSSION

Nestling mortality was slight after exclusion of that which could be attributed to predation. Occasionally all nestlings died due to unexplained causes which could include abandonment or death of parent or, conceivably, *Protocalliphora* feeding. However, nests in which all nestlings died before attaining 15 days of age were excluded from analysis because low parasite numbers in these nests could be attributable to the abbreviated period of host availability. In the remaining nests at Blodgett, 96.3% ($N =$

120) and 98.9% (N = 93) (Table 3) of these nestlings fledged in 1977 and 1978, respectively, while for Modoc County the corresponding figures were 93.2% (N = 280) and 97.9% (N = 488) (Table 4).

One-sample *t*-tests were performed to compare mortality in the most heavily infested nests with that in all nests from which at least one nestling fledged. Differences were not statistically significant at Blodgett Forest in 1977 and 1978 and in Modoc County in 1977. A statistically significant difference was found in Modoc County in 1978 (Table 4). Nests with mortality that year had an average infestation of 9.2 *Protocalliphora* per nestling. This is about 50% higher than overall average infestation of Modoc County but lower than that found at Blodgett each year.

Thus, high infestations may occasionally contribute to nestling mortality. However, the fact that no significant differences in nestling mortality were found between those heavily infested and all nests at Blodgett both years and in Modoc County in 1977 and that 93% of young in heavily infested Modoc nests fledged in 1978 suggest mortality attributable to *Protocalliphora* is slight. As noted, *Protocalliphora* numbers were low in nests where the entire clutch died before fledging indicating that it would be maladaptive for the parasites to kill their hosts. Further evidence of coevolution is suggested by the limited host range of many *Protocalliphora* spp. In our study we collected gravid females of several species of *Protocalliphora* in and around active chickadee nests but these species were never reared.

Although not evaluated in this study, post-fledging mortality may be due to the indirect effects of *Protocalliphora* infestations in the nest. Kluyver (Eschuis-van der Voet and Kluyver 1971) found reduced survival of Great Tits which fledged from nests heavily infested by *P. azurea*. Kluyver was working in isolated stands that reduced fledgling dispersal. In the Blodgett Forest and Modoc County plots, areas of vast contiguous forest, fledglings tend to disperse from the nest box plots and banding returns of these birds is 0.3% (Dahlsten and Copper 1979).

Eschuis-van der Voet (1972) and Eschuis-van der Voet and de Reede (1974) provided progress reports on their work which included a study on the effects of *P. azurea* on Great Tits. They noted a relationship between larval size and adverse effects on nestlings. These authors speculated that negative effects were most intense when the timing of oviposition resulted in the presence of large larvae when nestlings were near fledging. This supposition was based on evidence that *Protocalliphora* produced anemic conditions in nestling birds but that recovery could be rapid upon cessation of feeding by the parasites. However, fledglings in anemic condition would be less able to cope with post-fledging stresses. Whitworth (1976) also found rapid recovery could occur in nestlings unless hematocrit and hemoglobin levels fell below certain minima.

The bird work in Blodgett Forest and Modoc County was done entirely in the field. Blood analysis was deemed inappropriate because handling of nestlings after they reach an age of 14 days could cause premature fledging, and the critical period for assessing blood loss would be just prior to normal fledging. However, insight into the effects of *Protocalliphora* was gained by comparing biomass of parasites in a nest with that of their hosts.

Little work has been done on the blood volume, rate of hemopoiesis (especially under stress), and tolerance of blood loss in wild adult birds and less is known about nestlings. Several assumptions were employed to assess the degree of stress on nestling chickadees by *Protocalliphora* feeding. Mountain Chickadee adults weigh approximately 11 g (Dahlsten and Copper 1979), while adult Chestnut-backed Chickadees weigh about 10 g (Dahlsten, unpubl.). Growth rates of Mountain and Chestnut-backed chickadees are unknown, although they are comparable in size to Black-capped Chickadees (*Parus atricapillus*) for which daily weights during the nestling period are known (Kluyver 1961). By comparison with Kluyver's data, the average daily weight of a Mountain Chickadee would be 8.04 g. The blood volume in a bird is about 6% of body weight (J. Kaneko, pers. comm.), thus giving an average daily blood volume of 0.48 g.

To assess the amount of blood loss, the biomass of *Protocalliphora* must be converted to blood consumption. Johnson (1960) found that the immature stages of the bed bug *Cimex lectularius* had a conversion efficiency of ingested blood to biomass of 30–40%. Similar figures are not available for hematophagous Diptera, but K. S. Hagen (pers. comm.) considered 40% to be a reasonable and conservatively high figure (in terms of host impact). Using a biomass of 50 mg as an average biomass for larvae, each would therefore have consumed an average of 0.125 g of blood during the entire larval period. From this figure blood loss to *Protocalliphora* can be estimated (Tables 3, 4). The range was from 0.49 g per nestling in Modoc County in 1977 to 1.35 g per nestling in Blodgett Forest in 1978. The extreme case was a nest of Chestnut-backed Chickadees in Blodgett Forest which averaged 45.5 *Protocalliphora* per nestling. If each larva attained average size, the mean blood loss would have been 5.69 g per nestling.

Actual blood loss suffered by nestlings may fluctuate during the nestling period. The timing and synchrony of infestations varied although there was a tendency for larval numbers and sizes to be greater during the latter stages of the nestling period; this is the period considered by Eschuis-van der Voet and de Reede (1974) and Whitworth (1976) to be the most critical.

Kaneko (pers. comm.) believed that blood loss over 25% of daily volume should be fatal and that losses of 10% or more would have negative effects on the health and development of the bird. If the average daily blood

volume is 0.48 g, then average daily blood losses of 10 and 25% summed over the 21-day nestling period would mean total losses of 1.01 and 2.52 g of blood, respectively. This would mean that parasite loads exceeding eight *Protocalliphora* per nestling would have debilitating effects while loads exceeding 20 larvae per nestling would be severe enough to be fatal through blood loss. However, no mortality attributable to infestations occurred in the field, even though parasite loads often exceeded the above values. In the most heavily infested nest, blood loss was probably over 55% of the total blood volume. Similarly, Bennett (pers. comm.) reported biomasses of *Protocalliphora* two to three times that of their Barn Swallow hosts, yet no mortality was found in these nests. Since *Protocalliphora* larvae are, at present, known to be solely hematophagous, it is difficult to see how these nestlings survived.

While the assumptions here are speculative, it seems clear that nestlings in heavily infested nests are suffering a tremendous loss of blood. The ability of parent birds to counteract this drain on the nestlings' energy reserves is not known. To some extent, partial recovery may occur with the cessation of parasite feeding (Whitworth 1976) and the continued provision of food by the parents after fledging (Ricklefs 1974). However, nestling development is not uniform; consequently, stresses at specific times may lead to retardation of organs or tissues without the possibility for complete compensation even if the stress is later alleviated (O'Connor 1977). First year mortality of Mountain Chickadees has been calculated at 85% (Dahlsten and Copper 1979) and it is likely that much of this mortality occurs shortly after fledging as young inexperienced birds are confronted with many new stresses. These stresses might be aggravated in birds weakened by *Protocalliphora* and fledging in a somewhat anemic condition. Additionally, post-fledging success has been positively related to body size in a related species, *Parus major* (Perrins 1965, Garnett 1981). If blood loss from *Protocalliphora* feeding does, in fact, retard nestling growth, heavily attacked birds will be further disadvantaged upon fledging and still more likely to succumb.

SUMMARY

More than 90% of Mountain (*Parus gambeli*) and Chestnut-backed (*P. rufescens*) chickadee nests in two interior California mixed conifer habitats were found to be infested with *Protocalliphora* parasites. In contrast, only 1 of 55 chickadee nests was infested in a coastal study area. Failure of most puparia in this nest to develop may reflect the presence of some environmental factor unsuitable for *Protocalliphora*. Infestation numbers varied considerably, and in one instance the hosts fledged despite an infestation exceeding 45 *Protocalliphora* per nestling. Nestling mortality was low and did not seem to be related to effects of the parasites. This observed result was surprising in light of expected effects predicted from

parasite biomasses supported by many nestlings. However, fledglings stressed by blood losses resulting from heavy *Protocalliphora* infestations are nonetheless thought to have reduced post-fledging success.

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LITERATURE CITED

- BÉDARD, J. AND J. N. MCNEIL. 1979. *Protocalliphora hirudo* (Diptera: Calliphoridae) infesting Savannah Sparrow, *Passerculus sandwichensis* (Aves: Fringillidae) in eastern Quebec. *Can. Entomol.* 111:111-112.
- BENNETT, G. F. 1957. Studies on the genus *Protocalliphora* (Diptera: Calliphoridae). Ph.D. diss. Univ. Toronto, Toronto, Ontario, Canada.
- DAHLSTEN, D. L. AND W. A. COPPER. 1979. The use of nesting boxes to study the biology of the Mountain Chickadee (*Parus gambeli*) and its impact on selected forest insects. Pp. 217-260 in *The role of insectivorous birds in forest ecosystems* (J. G. Dickson et al., eds.), Academic Press, Inc., New York, New York.
- ESEHUIS-VAN DER VOET, C. W. 1972. Parasitism by *Protocalliphora azurea* (Fall). *Verh. K. Ned. Akad. Wet. Afd. Natuurk de Tweede Reeks* 61(3):73-74.
- AND H. N. KLUYVER. 1971. Parasitism by *Protocalliphora azurea* (Fall). *Ibid.* 60: 50-51.
- AND R. H. DE REEDE. 1974. The effect of parasitism by *Protocalliphora*. *Ibid.* 63: 77-79.
- FRAENKEL, G. 1952. The role of symbionts as sources of vitamins and growth factors for their insect hosts. *Tijdschr. Entomol.* 95:183-195.
- GARNETT, M. C. 1981. Body size, its heritability and influence on juvenile survival among Great Tits, *Parus major*. *Ibis* 123:31-41.
- GOLD, C. S. AND D. L. DAHLSTEN. 1983. The incidence, habitat selection, and biology of *Protocalliphora* (Diptera: Calliphoridae) found in the nests of Mountain and Chestnut-backed chickadees in California. *USDA Tech. Bull.*, In Press.
- JOHNSON, C. G. 1960. The relation of weight of food ingested to increase in body weight during growth of the bed-bug, *Cimex lectularius* L. (Hemiptera). *Entomol. Exper. and Appl.* 3:238-240.
- KLUYVER, H. N. 1961. Food consumption in relation to habitat in breeding chickadees. *Auk* 78:532-550.
- LACK, D. 1966. *Population studies of birds*. Clarendon Press, Oxford, England.

- O'CONNOR, R. J. 1977. Differential growth and body composition in altricial possessives. *Ibis* 119:147-166.
- PERRINS, C. M. 1965. Population fluctuations and clutch size in the Great Tit, *Parus major*. *J. Anim. Ecol.* 34:601-647.
- RICKLEFS, R. E. 1974. Energetics of reproduction in birds. Pp. 252-297 in *Avian energetics* (R. A. Paynter, ed.). Publ. Nuttall Ornith. Club No. 15. Cambridge, Massachusetts.
- ROTHSCHILD, M. AND T. CLAY. 1952. Fleas, flukes, and cuckoos, a study of bird parasites. Collins, London, England.
- WELTY, J. C. 1962. *The life of birds*. W. B. Saunders Co., Philadelphia, Pennsylvania.
- WHITWORTH, T. L. 1976. Host and habitat preferences, life history, pathogenicity and population regulation in species of *Protocalliphora* Hough (Diptera: Calliphoridae). Ph.D. diss. Utah State Univ., Logan, Utah.
- ZUMPT, F. 1965. *Myiasis in man and animals in the old world*. Butterfield Inc., Washington, D.C.

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The Wilson Ornithological Society will hold its 1984 Annual Meeting at the University of North Carolina, Wilmington, in conjunction with the Annual Meeting of the Carolina Bird Club, 31 May-3 June. JAMES F. PARNELL, Biology Department, University of North Carolina, Wilmington, NC 28401, is chairing the local committee. MARY H. CLENCH, 2239 NW 21st Ave., Gainesville, FL 32605, will guide the scientific program.